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A LIMNOLOGICAL INVESTIGATION OF THE
DYNAMICS OF A SANDY, WAVE-SWEPT
SHOAL IN DOUGLAS LAKE, MICHIGAN*

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Barren, sandy, wave-swept shoals in certain lakes have often been considered biological deserts because of the supposed paucity of organisms inhabiting them. It was the purpose of this investigation to study the environmental dynamics which affect the habitat and behavior of organisms on such a shoal and to correlate the results of a qualitative and quantitative study of shoal bottom fauna with these dynamics.

Very little has been written about such shoals. Kreckler and Lancaster (1933) found sandy shoals in western Lake Erie the least productive of several types studied. Muttkowski (1918) mentioned the sparse, burrowing assemblage of organisms on sandy shoals of Lake Mendota and related its scarcity to waves and molar action. Rawson (1930) stated that sandy, wave-swept shoals in Lake Simcoe are very sparsely inhabited. Other authors have mentioned the scarcity of organisms on shoals of this type.

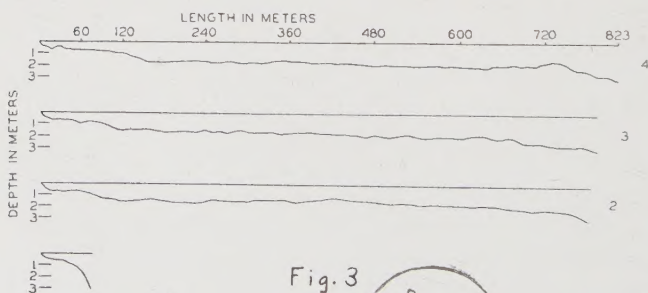
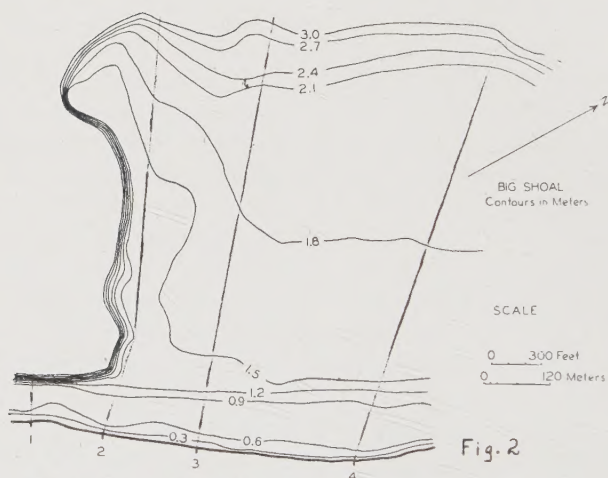
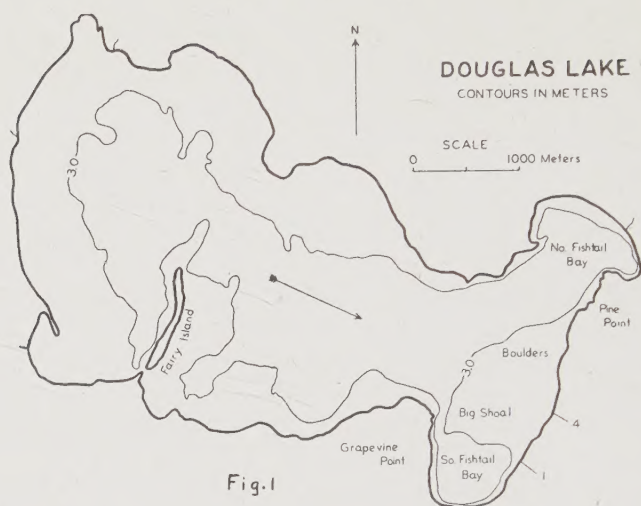
That environmental conditions on sandy, wave-swept shoals are very rigorous is attested by the direct effects of these conditions on organisms. For example, Brown, Clark and Gleissner (1938) found that the size of certain Naiades in the same age classes varied with degree of exposure in Lake Erie. Kreckler (1924) showed the occurrence of *Goniobasis livescens* to be influenced by degree of exposure and according to Wiebe (1926), the obesity of this snail is directly proportional to the same factor.

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this investigation; and to Dr. Ruth Marshall, Dr. Herbert H. Ross, Dr. Jacob Rempel, Dr. Elmer Berry, Dr. Henry Van der Schalie and Mr. K. E. Goellner for identifications of materials.

METHODS

Bottom samples were taken along four transects (Fig. 2) at depth intervals of 0.3 meter with a Peterson dredge enclosing an area of one-thirteenth square meter. Two dredge hauls constituted a sample. Such a sample was washed in a pan screen of 30 mesh per inch. Residues were preserved in 10 per cent formalin.

Bottom samples were sorted with the aid of the calcium chloride method (Beak, 1938). This dense solution caused all Arthropoda, excepting Trichoptera in sand-covered cases, to float to the surface when the sample was stirred. Annelida and some Mollusca were poured off after vigorous stirring and before settling could occur. The supernatant liquid was poured through a piece of fine marquisette stretched over a funnel. All organisms significant to this work and some debris were retained. The sample was then carefully scrutinized for organisms missed in the chloride treatment. The residue was washed into a finger bowl and examined with a binocular dissecting microscope.

The calcium chloride method removed approximately 98 per cent of the Arthropoda (Trichoptera excepted) and 95 per cent of the Annelida. Mollusca were effectively removed only when very small. This method was suitable when bottom materials consisted of gravel, sand or other heavy substances.

To test the rate of bottom shifting wooden frames, 60 by 60 by 15 cm., were set in the bottom at water depths of 0.3, 0.6, and 0.9 meter. These frames were buried until the upper edge was flush with the surface of the bottom, cleaned out and left to fill with drifting bottom material. The time required for the frames to become filled was noted.

To determine the amounts of various materials constituting the bottom at different depths, bottom samples were collected at water's edge, and 0.5, 1.0, 1.5, and 2.0 meters depth. A 500 cc. portion of each was washed through a stack of six Tyler Standard Scale Screens of 4.7, 2.4, 1.2, 0.4, 0.2,

FIG. 1. Map of Douglas Lake showing that portion of Big Shoal, between the numbers 1 and 4 on which this study was conducted. Only the shallow-water contours in the lake are indicated.

FIG. 2. Detailed map of Big Shoal. Dotted lines represent transects along which bottom samples were taken and profiles made. The numbers 1, 2, 3, and 4 designate the transects. Contours correspond to depth intervals used in sampling.

FIG. 3. Bottom profiles on Big Shoal. The numbers on the right of each profile corresponds with like numbers in Figure 2, which show the locations of these profiles.

and 0.15 mm. square mesh aperture. Material retained by each screen was measured volumetrically.

Direction of water current was determined by an apparatus modified from that of Scott (1916) and a rod fitted with pieces of fine silk ribbon 30 cm. long, spaced at intervals of 30 cm. along it. The rod was forced into the bottom and allowed to stand by itself. Currents were detected by watching the behavior of the ribbons at various levels.

SITUATION STUDIED

Limnological features of Douglas Lake have been described by I. D. Scott (1921), Reighard (1915), Welch (1927), Eggleton (1931) and others; hence no general account is necessary here. The significant features of Big Shoal on which this work was done are portrayed in Figs. 1, 2, and 3.

For purposes of this study the 3.0-meter contour and lines numbered 1 and 4, Fig. 1, are considered as the lakeward boundaries of Big Shoal. When so limited, the surface area is 119.4 acres (483,000 square meters). Using 712.0 feet above sea level as the average lake surface elevation, the volume of water overlying Big Shoal is 830,000 cubic meters (673 acre feet).

Profiles of Big Shoal made at transects marked 1, 2, 3, and 4 (Fig. 2) are shown in Fig. 3, and no detailed description is needed here.

PHYSICAL FEATURES

The winds most effective in producing waves which influence Big Shoal are, in order of importance, from the northwest, west, southwest, and north. Northwest winds are most effective since they sweep the maximum length of the lake and are consistently of greater velocity. Big Shoal is almost constantly influenced by winds during the season of open water. Winds on Douglas Lake tend to be cyclic, except during heavy storms. They are strongest during the afternoon, decrease toward evening and reach a calm at night which persists well into the following morning. The maximum total wind movement for each direction in any one day during this study is as follows: North, 600 miles or 25 per hour; northwest 564 miles or 24 per hour; west, 578 miles or 24 per hour; southwest, 471 miles or 20 per hour and northeast, 458 miles or 19 per hour. There have been a few days of dead calm on Douglas Lake during the period of this investigation. At no time was a calm observed to continue more than two days.

Air temperatures in the Douglas Lake region vary through a range of about 60.0°C. during an average year. The monthly and yearly weather summaries for Mackinaw City in the Michigan Section of Climatological Data, United States Department of Agriculture Weather Bureau show the highest temperatures for 1937 and 1938 at 33.9°C. and 35°C. respectively. Lowest temperatures for the same years were -19.4°C. and -27.2°C. A detailed table of data from the same source is on file in the Graduate

School, University of Michigan. July and August are the hottest months. Should high temperatures registered in these months persist over several days, their effect upon shallow waters and the bottom organisms under them might be disastrous. Such an instance is on record for the year 1936, when temperatures at Douglas Lake rose above $37.8^{\circ}\text{C}.$, six days in succession July 8–13 (Gates 1938).

Wave action is one of the most influential factors in the dynamics of Big Shoal. There are waves or wave-formed currents moving over it almost constantly. According to a formula for wave height given by Stevenson (1886), the height of waves which might be produced by a northwesterly wind on Big Shoal is calculated at 2.9 feet (0.88 meter). Wave lengths of more than 25 feet (7.6 meters) are rare for this lake; they average about 10 to 20 feet (3.0 to 6.1 meters) for storm conditions.

Two types of wave action occur on Big Shoal, one, oscillatory, in which no forward movement of water occurs and the other, translation, in which actual forward movement of water takes place. The oscillatory wave action is of little consequence. Waves of translation are more effective on the shoal and they set in motion practically all of the currents active there. These currents are of two principal types, alongshore and undertow or return currents.

Currents which affect Big Shoal travel in different directions depending on wind direction. Currents, as measured during a stiff northwest wind, are mainly on-shore. They meet the shore almost at right angles and result in a definite, measurable undertow at water depths of 1.0 meter. In addition, there are developed along-shore currents flowing to both North and South Fishtail Bays. Currents animated by a stiff north wind, develop into powerful alongshore flowages off Big Shoal into South Fishtail Bay. No undertow is detectable. West and southwest winds set in motion currents which affect the northeast end of Big Shoal. Alongshore currents sweep into North Fishtail Bay.

Ice on Douglas Lake usually becomes 18–26 inches (45–66 cm.) thick. Greater thicknesses (0.77 meter) have been reported. Along the shore of Big Shoal, ice may freeze to the bottom. The bottom itself presumably freezes to some depth below the ice. Whether organisms on these areas of Big Shoal are able to withstand such freezing is not known. The faunal distribution following disappearance of the ice cover indicates catastrophic conditions.

The ice cover on Douglas Lake affects the shores and shallow regions by pushing. There are two ways in which ice pushing takes place: expansion and contraction due to temperature changes and ice jams resulting from winds. Both affect Big Shoal but the ice jams are more influential.

The average annual temperature range of water covering Big Shoal is $0.0^{\circ}\text{C}.$ – $29.0^{\circ}\text{C}.$ Summer extremes may occasionally be higher. On July 8

beach where it forms an elevation which is almost level. There may be a rather abrupt slope from the top of this elevation to the water during periods of inconsequential wave action. Heavy storm waves push this elevation backward from the water's edge toward the permanent bank and in such a position, it becomes a lasting addition to the outer beach. Measurements made on a stake near shore in 0.16 meter of water in early May showed a deposition of sand 0.2 meter deep and 4.5 meters wide above the original watermark by late August. This beach building is repeated annually. Portions of the built beaches are removed each year by winds and are lost to the lake.

Transitory minor beach formations result from moving bottom materials on Big Shoal. Onshore parallel waves may form regular beach cusps, the size and spacing of which depends upon the magnitude of the waves. Johnson (1919) states that slight irregularities in the beach seem to initiate the formation of such cusps and the development of them to full size depends upon currents in the backwash of parallel waves. A switch in wind direction toward the north after a west or northwest blow soon erases the cusps, but their bases may serve as anchors or starting points for many small spits which also disappear soon after forming if the north wind continues. Bars are often formed wherever alongshore currents are deflected lakeward by shoreline irregularities. However, they are ephemeral in nature and disappear with each change in wind direction.

It is evident that bottom materials in the shallower regions of Big Shoal are moved back and forth by the variously directed currents and waves. Storms of long duration permanently remove sand and finer constituents from the shoal. What might appear to be a rapid transport of materials off the shoal by a brief storm is more often a temporary shifting of position.

The counteraction of different current directions retards the process of shoal extension but permanent trends are toward the south margin of the shoal. During the summer and late autumn, prevailing northwest winds create waves and currents which carry sand from the middle of Big Shoal toward the southern margin. A bar is built lakeward along this margin and becomes 80–100 meters long by late autumn. Waves and currents initiated by early spring winds from the north, beat directly upon this bar sweeping it into South Fishtail Depression early in the season.

BIOLOGICAL FEATURES

The water covering Big Shoal is inhabited by the usual surface plankters found in Douglas Lake. That they are of some importance as food for certain bottom-dwelling organisms is well known. Occasional drifts of these plankters are concentrated in shallow water by gentle onshore waves.

The bulrush, *Scirpus occidentalis* (Wats.), is the dominant emergent plant growing on Big Shoal. Its extent is restricted to two patches; one just

south of, and extending along with, transect two (Fig. 2) and another in shallow water north of transect four. The former patch extends northwest as a weak narrow stand to transect three about 300 meters out from shore. Other rooted plants on the shoal proper consist of a few scattered patches of a very short, low-growing, red-leaved *Potamogeton*, probably *P. heterophyllus*, and some rather extensive dense beds of *Chara* and *Najas flexilis* (Willd.) in water 2.1–3.0 meters deep on the lakeward margin of the shoal, especially between transects three and four (Fig. 2). The declivity along the southwest margin of Big Shoal is rimmed with a narrow belt of plants which may become rather dense. Dominant in this situation is *Potamogeton natans* Linnaeus.

QUALITATIVE FEATURES OF FAUNA

The organisms collected on Big Shoal in bottom samples during this study are listed below. Only the macroscopic fauna was considered. Some of the genera were grouped together for the purpose of quantitative work. Where this was done, the genera involved are listed under the group heading and annotations given for the group only, not for the individual genera or species.

Coelenterata

Hydra sp.—probably *H. oligactis* Pallas; found in association with *Chara* and sometimes stones at 1.8–3.0 meter water depths; not typical; rare.

Platyhelminthes

Planaria spp.—present on stones in deeper areas, 2.1–3.0 meters; rare.

Nemathelminthes

Nematoda.—not identified and not considered. Because of their small size, they passed through screen used to concentrate samples; common.

Bryozoa

Plumatella sp.—scattered over shoal; on *Chara*; rare.

Annelida

Stylaria.—at depths 1.5–3.0 meters; usually associated with *Chara*; rare.

Pristina.—at depths 1.5–3.0 meters; usually associated with *Chara*; rare.

Limnodrilus.—generally distributed; abundant.

Tubifex.—at depths 2.4–3.0 meters; associated with sandy, mucky areas; rare.

Enchytraeus.—generally distributed; prefers depths 1.5–2.4 meters; rare.

Sparganophilus eiseni F. Smith.—one specimen taken.

Glossiphonia.—probably not typical; very rare.

Mollusca

Valvata tricarinata Say.—occurs consistently at depths of 1.8–3.0 meters; mostly at depths of 2.7–3.0 meters; rare.

Campeloma.—generally distributed; most abundant at southwest end of shoal; rare. Two species, *C. decisum* (Say) and *C. rufum* (Haldeman).

Amnicola.—restricted to areas beneath 1.8–3.0 meters of water; most numerous at depths of 2.4–3.0 meters; abundant. Two species, *A. limosa* Say and *A. lustrica* Pilsbry.

Lymnaea.—occasional immigrants; at depths 2.7–3.0 meters; not typical; rare. Two species, *L. obrusa* Say, and *L. stagnalis* (Say).

Stagnicola emarginata (Say).—at depths 2.4–3.0 meters; rare.

Gyraulus parvus (Say).—restricted to depths 1.8–3.0 meters; very abundant.

Helisoma.—not typical; very rare. Two species, *H. antrosa* (Conrad) and *H. campanulata Smithii* (F. C. Baker).

Physa parkeri DeCamp.—at depths of 2.4–3.0 meters; not typical; 43 specimens shown on population tables.

Anodonta grandis Say.—at depths 2.1–3.0 meters; mucky bottom preferred; mostly very small young, 2–4 mm. in length; rare.

Ligumia nasuta (Say).—one adult taken on Big Shoal; mostly very small young, 2–3 mm. in length; rare.

Lampsilis siliquoidea (Barnes).—at depths 1.5–3.0 meters, occasionally found in shallows; many young, 2–3 mm. long; predominant mussel on Big Shoal.

Sphaerium spp.—at depths 0.2–1.2 meters; rare.

Musculium spp.—at depths 2.0–3.0 meters; rare.

Pisidium spp.—generally distributed; common.

Arthropoda—Crustacea

Hyalella azteca (Saussure).—at depths 2.1–3.0 meters; mostly associated with plants; abundant.

Cambarus.—juveniles only; not typical; very rare. Two species, *C. propinquus* Girard, and *C. virilis* Hagen.

Arthropoda—Hydracarina

Limnesia.—generally distributed; common. Two species, *L. fulgida* Koch, and *L. maculata* (Müll.).

Limnesiopsis anomala Koen.—not typical; very rare.

Hygrobatas.—depths 1.2–2.1 meters preferred; rare. Two species included in group: *H. longipalpis* (Herm.) and *Unionicola crassipes* (Müll.).

Lebertia.—most prevalent at depths 0.9–1.8 meters; rare; included in group: *L. porosa* Thor and *Oxus elongatus* Mar. (new record for Michigan).

Piona.—at depths 2.4–3.0 meters; associated with plants; three species: *P. pugilis* (Wol.), *P. reighardi* (Wol.) and *Forellia* sp. nov.

Mideopsis.—generally distributed; rare; includes two species: *M. americanus* Mar. and *Koenikea spinipes* (Wol.).

Arrhenurus.—depths 1.2–3.0 meters preferred; rare; includes two species: *A. bicaudatus* Mar. and *Krendowskia similis* Viets.

Arthropoda—Insecta

Sialis.—taken twice during study; very rare.

Ephemera.—generally distributed but prefers loose sand or mucky bottom; rare.

Ephemerella.—probably not typical; very rare.

Hexagenia.—generally distributed; rare.

Baetisca.—found but once; 0.6 meter depth.

Baetis.—occurs at depths of 1.2–1.8 meters; very rare.

Brachycercus.—occurs at depths of 2.1–3.0 meters; very rare.

Cloeon.—occurs at depths of 0.6–1.5 meters; very rare.

Caenis.—generally distributed; prefers depths of 1.2–2.4 meters; common.

Anisoptera.—few individuals in association with *Chara*.

Macromia.—prefers depths of 0.6–1.8 meters; rare.

Hagenius.—distribution same as *Macromia*; rare.

Gomphus.—generally distributed; prefers depths 1.6–2.7 meters; rare.

Progomphus.—limited to shallow water, 0.0–0.9 meter deep; common.

Trichoptera.—generally distributed over shoal; prefer plant inhabited areas; common. Larval forms represented are:

Polycentropidae (2 species)

Oecetis inconspicua

Oecetis cinerascens

Leptoceridae (2 species)

Leptocella (2 species)

Athripsodes sp.

Triaenodes sp.

Molanna uniophila

Mystacides longicornis

Coleoptera.—two kinds found; Elmidae and what appears to be *Berosus*.

Eriocera.—taken once at 3.0 meters depth; very rare.

Chaoborus.—generally distributed at depths of 1.5–3.0 meters; scattered; rare.

Hemerodromia.—shallow water preferred; very rare.

Tabanus.—generally distributed at 0.3–1.5 meters depth.

Atherix.—distribution same as *Tabanus*; rare. Johannsen (1935) states that the larvae of this genus have been found only in streams.

Tanytarsus.—generally distributed but show definite preference for water deeper than 0.9 meter; most numerous group inhabiting Big Shoal.

Chironomus.—generally distributed; second most abundant group on Big Shoal; representatives of the following subgenera were found:

Cryptochironomus

Allochironomus

Spaniotoma (Orthoclaadiinae)

Limnochironomus

Polypedilum

Glyptotendipes

Endochironomus

Chironomus (s. str.)

Pseudochironomus

Palpomyia.—prefers water depths 0.3–2.1 meters; common; includes *Dasyhleia* group.

Pentaneura.—generally distributed at depths 1.2–3.0 meters; common.

Procladius.—(recently revised to include *Protenthes*); generally distributed; common.

Fishes inhabiting Big Shoal are discussed at length by Reighard (1915). No further mention of them need be made here.

The following discussion and analysis of the bottom fauna of Big Shoal is based upon results obtained from 299 quantitative bottom samples. Approximately 30 samples were taken from the shoal at each collection date, excepting Oct. 9, Oct. 31, 1937, and May 8, 1938 when 19, nine, and 15 samples, respectively, were secured. Practically all of the groups in the annotated list were treated quantitatively in this study. Complete tabulations of the shoal population as found on each collection date are on file in the Graduate School, University of Michigan. Only the ten most common genera are considered here. The omission of minor groups does not seriously distort the results.

DEPTH DISTRIBUTION

Depth distribution of organisms on Big Shoal has been summarized in the annotated list. From the list and Tables 1–10, it is very evident that most organisms are excluded from the shallow regions (0.0–0.9 meters). However, *Progomphus* is found only in that zone. The mollusca, *Amnicola* and *Gyraulus* are practically absent from waters shallower than 1.5 meters. *Pisidium*, although slightly less abundant at the 0.3-meter and 0.6-meter depths, are uniformly distributed over the shoal. Other genera occur in shallow water to a varying degree but all are less numerous from the 0.9-meter depth shoreward. There is a general increase in numbers of organisms with increasing water depth. Beyond 2.7 meters, however, a consistent decrease is evident. This decrease is due, in part to the declivity surrounding Big Shoal. Transition from the littoral to benthic habitat occurs rapidly beyond 2.7 meters depth.

TABLE 1. Numbers of *Limnodrilus* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	52	32	—	—	—	—	—	—	—	7	8	2
0.6	57	—	—	3	—	—	—	2	9	75	122	68
0.9	218	97	3	74	—	11	88	120	75	119	237	343
1.2	176	143	49	147	70	106	358	126	290	187	213	341
1.5	165	147	99	125	259	152	220	211	112	224	165	304
1.8	205	190	180	254	297	139	374	258	368	165	216	251
2.1	—	—	211	214	272	370	269	656	176	45	128	233
2.4	—	—	156	205	246	249	270	346	302	222	187	167
2.7	—	—	157	—	117	227	291	385	306	231	247	189
3.0	—	—	58	33	96	251	215	158	218	330	224	123
Totals	873	609	913	1055	1357	1505	2085	2262	1856	1605	1747	2021
Average	146	102	91	117	136	151	209	226	186	161	175	202

TABLE 2. Numbers of *Ammicola* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	—	—	—	—	—	—	—	—	—	—	—	—
0.6	—	—	—	—	—	—	—	2	—	—	—	—
0.9	—	—	—	—	—	—	—	—	—	—	2	—
1.2	—	—	—	—	—	—	—	—	—	—	2	—
1.5	—	7	—	—	—	—	—	—	4	—	2	22
1.8	22	150	—	—	—	2	—	17	51	42	4	134
2.1	—	—	2	—	—	48	—	3	101	77	17	167
2.4	—	—	—	128	58	42	61	81	79	53	22	95
2.7	—	—	96	—	124	73	102	118	88	73	34	266
3.0	—	—	131	19	70	51	115	117	116	74	40	165
Totals	22	157	229	147	252	216	278	338	439	319	123	849
Average	4	26	23	16	25	22	28	34	44	32	12	85

TABLE 3. Numbers of *Gyraulus* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	—	—	—	—	—	—	—	—	—	—	—	—
0.6	—	—	—	—	—	—	—	—	—	—	—	—
0.9	—	—	—	—	—	—	—	3	—	—	5	—
1.2	—	—	—	—	—	—	—	—	—	—	—	—
1.5	—	2	—	—	—	—	—	—	—	—	—	222
1.8	70	65	—	—	—	—	—	—	97	73	64	368
2.1	—	—	—	—	10	24	7	3	209	115	126	992
2.4	—	—	39	54	109	196	95	200	231	211	209	1025
2.7	—	—	106	—	371	141	221	101	75	271	190	1241
3.0	—	—	151	—	51	73	61	55	187	189	108	997
Totals	70	67	296	54	541	434	384	362	799	859	702	4845
Average	12	12	30	6	54	43	38	36	80	86	70	485

TABLE 4. Numbers of *Pisidium* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	52	29	—	—	3	—	—	11	9	44	99	7
0.6	59	7	—	93	57	20	53	31	42	13	22	—
0.9	57	65	13	58	3	15	22	61	44	22	35	44
1.2	49	45	13	3	33	26	19	77	51	50	59	22
1.5	37	20	26	29	16	55	18	42	154	51	110	35
1.8	46	26	73	26	35	7	4	38	31	53	33	64
2.1			25	26	48	44	13	42	37	58	38	31
2.4			39	29	22	13	9	75	71	51	44	35
2.7			35		13	24	13	38	46	115	44	40
3.0			35	26	22	22	26	18	42	48	35	68
Totals	300	192	259	290	252	226	177	433	527	505	519	346
Average	50	32	26	32	25	23	18	43	53	51	52	35

TABLE 5. Numbers of *Hyalella* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	3	10	—	—	—	—	—	2	2	—	—	—
0.6	7	—	—	—	2	—	—	—	42	26	20	57
0.9	42	130	—	10	3	—	11	8	13	35	54	97
1.2	183	195	—	6	7	—	10	18	35	70	55	222
1.5	130	51	13	29	19	55	15	42	181	141	119	192
1.8	645	97	108	188	114	24	20	36	150	53	81	332
2.1			62	65	74	33	16	35	13	3	21	328
2.4			65	22	3	114	48	29	389	220	213	1140
2.7			42		39	114	55	217	280	609	203	163
3.0			99	32	38	86	122	42	7	550	152	49
Totals	1010	483	389	352	299	426	297	429	1112	1707	918	2580
Average	168	81	39	39	30	43	30	43	111	171	92	258

TABLE 6. Numbers of *Limnesia* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	3	61	3	—	—	—	4	7	—	2	10	9
0.6	38	13	—	19	—	2	11	9	9	26	24	82
0.9	179	195	3	35	3	15	42	110	16	11	122	172
1.2	20	33	31	134	101	29	67	33	46	15	31	110
1.5	24	291	64	122	93	46	11	27	15	2	13	20
1.8	33	123	55	19	15	11	13	29	2	4	2	37
2.1			42	39	10	37	16	16	7	—	6	53
2.4			7	58	29	46	46	22	13	4	5	29
2.7			45		52	37	22	42	9	11	6	64
3.0			55	91	58	26	32	11	22	16	4	53
Totals	297	716	305	517	361	249	264	306	139	91	223	629
Average	50	119	31	57	36	25	26	31	14	9	22	63

TABLE 7. Numbers of *Chironomus* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	287	80	—	—	—	9	75	128	13	26	30	418
0.6	207	84	—	38	59	68	222	104	167	394	134	150
0.9	253	149	166	454	138	123	202	144	115	405	186	229
1.2	68	71	90	90	128	70	173	141	97	361	174	222
1.5	66	145	64	128	64	68	165	112	130	356	200	139
1.8	346	318	77	52	46	81	198	133	191	262	154	227
2.1			75	85	163	304	534	291	194	195	101	224
2.4			188	186	166	359	579	235	345	277	132	277
2.7			275	267	337	960	251	264	616	182	154	154
3.0			317	52	259	482	784	251	317	544	141	128
Totals	1227	847	1252	1085	1290	1901	3892	1790	1833	3436	1434	2168
Average	205	141	125	121	129	190	389	179	183	344	143	217

TABLE 8. Numbers of *Palpomyia* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-18 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	34	406	—	—	—	2	4	2	2	2	22	17
0.6	101	26	—	6	15	2	57	4	13	13	134	134
0.9	109	247	16	48	10	18	807	52	13	48	51	145
1.2	59	156	24	86	95	59	589	24	2	13	33	123
1.5	70	101	44	99	96	139	524	29	4	20	4	37
1.8	51	52	86	65	81	48	266	8	7	13	—	31
2.1			70	124	147	103	163	13	7	3	17	29
2.4			78	35	13	46	46	13	9	—	4	7
2.7			32		13	35	77	21	16	13	7	11
3.0			16	59	16	57	22	13	8	16	9	20
Totals	424	988	366	522	486	509	2555	179	81	141	281	554
Average	71	165	37	58	49	51	256	18	8	14	28	55

TABLE 9. Number of *Procladius* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	46	118	—	—	—	—	—	—	—	—	34	117
0.6	40	13	—	19	7	18	18	2	—	11	16	163
0.9	64	59	—	96	16	11	53	3	—	9	27	134
1.2	26	32	59	80	75	37	29	2	2	57	20	75
1.5	22	59	31	61	86	51	26	2	40	57	22	9
1.8	92	19	33	26	11	33	4	3	11	46	59	4
2.1			32	52	22	46	6	3	11	45	34	11
2.4			91	118	35	103	13	2	16	75	123	7
2.7			147		26	57	16	3	22	139	55	4
3.0			19	—	13	88	19	9	31	93	143	11
Totals	290	300	412	452	291	444	184	29	133	532	533	535
Average	48	50	41	50	29	44	18	3	13	53	53	54

TABLE 10. Number of *Tanytarsus* per square meter as found on Big Shoal during this study.

Depth in meters	Oct. 9-10 1937	Oct. 31 1937	Apr. 23 1938	May 8 1938	May 14-15 1938	May 28-29 1938	June 17-19 1938	July 2-4 1938	July 16-17 1938	July 30-31 1938	Aug. 13-15 1938	Sept. 13-14 1938
0.3	1	19	—	—	10	2	—	—	2	—	13	—
0.6	11	—	—	3	24	—	110	7	125	104	293	103
0.9	32	59	3	3	99	9	46	123	125	596	427	185
1.2	73	214	2	22	42	20	237	66	51	196	123	165
1.5	539	816	31	16	38	112	158	134	209	282	297	491
1.8	1703	2639	253	631	202	436	711	405	345	301	205	583
2.1			941	1008	3053	3043	1923	922	260	483	235	1120
2.4			2347	909	1894	2449	1419	858	493	647	187	1045
2.7			2240		1534	2534	1952	640	655	898	207	777
3.0			1613	39	1053	2431	1334	293	524	752	275	688
Totals	2359	3747	7430	2631	7949	11036	7890	3448	2789	4259	2262	5157
Average	393	625	743	292	795	1104	789	345	279	426	226	516

SEASONAL VARIATION

The most striking seasonal effect in the bottom fauna as determined from consideration of the entire tabulation of bottom samples is the appearance of additional species during the progress of summer. Certain groups, whose populations are consistently low, occasionally appear in samples and consideration of their seasonal variation is not possible because of insufficient representatives. Other groups enter the population in spring, persist throughout summer and reach their maximum development before the inclemency of approaching winter causes them to disappear. Among the most notable of these are *Hydra* and the Oligochaeta: *Pristina* and *Stylaria*.

The average bottom population per square meter increases gradually during the months of April, May and June. A significant drop in numbers occurs in early July and continues throughout the month. There is a secondary rise in early August. The minimum in seasonal abundance is reached by mid-August. By mid-September, the average number of individuals per square meter has increased to a seasonal maximum. Undoubtedly, winter conditions reduce the number of individuals per unit area. Comparison of April collections with those made in September bears out this conclusion (Tables 1-10).

Quantitative seasonal variation in the 10 most numerous groups of organisms found is shown in Tables 1-10. There is a general population minimum in late summer for every group considered. Each group varies independently due to a definitive pattern of environmental and life history factors which will be discussed later in detail. *Limnodrilus* shows a gradual increase in numbers per square meter from early spring until late July and early August. The decline at this time is not sharp but is significant. Mid-September samples indicate an addition to the population although the increase is not pronounced. Average numbers per square meter of *Amnicola* remain almost constant during spring and summer, increase somewhat in

July but drop to their season's lowest ebb in mid-August. Mid-September samples show a maximum in the seasonal population of this group. *Gyrulus* parallels *Amnicola* in seasonal distribution. However, its numbers do not decrease as markedly in mid-August. The population of *Pisidium* increases gradually into mid-summer and maintains an almost constant level until mid-September decreasing somewhat at that time and continuing to decrease into October. The population of *Hyalella* remains fairly constant throughout the early months of spring and summer. It rises very rapidly in July and descends just as abruptly to a minimum in mid-August. The maximum for this genus was reached in September. Numbers of *Limnesia* are high in spring and autumn; being lowest in late July. The population of *Procladius* ebbs in July but remains constant throughout the remainder of the season. Numbers per square meter of *Tanytarsus* are high at all times but they reach a peak late in May which is followed by a gradual decrease from early July to August when a secondary rise in the population occurs. Another low in population appears in mid-August. Mid-September samples show a definite population increase. Because it is so large, fluctuations in abundance of this group determine the general population pattern of the shoal. Two maxima are shown by the counts of *Chironomus*. One maximum occurs in mid-June and another in early August. The population of *Palpomyia* increases from early spring to mid-June where it reaches an enormous high. Immediately following this high the population almost disappears in July. There is a gradual increase in numbers from early August through October.

FACTORS AFFECTING SEASONAL VARIATION AND DEPTH DISTRIBUTION

Water temperature becomes a controlling factor in distribution as it approaches the extremes of its annual fluctuation. Minimum temperatures are less effective on Big Shoal. Still, minimum temperatures determine the depth of ice cover and the freezing of the bottom near shore, thus exerting an indirect influence on organisms inhabiting that region. Maximum temperatures may exceed the threshold of toleration of certain organisms on Big Shoal. The population minimum in August is due, in part, to the influence of the high water temperatures which prevail during that month. It is known that such forms as *Limnodrilus*, *Limnesia* and *Amnicola* may be virtually exterminated by unusually high summer water temperatures. Accompanying the seasonal rise in water temperatures on Big Shoal there is an increase in metabolic activity and life-history progression rate of the organisms inhabiting it. This rise probably determines the appearance of seasonal forms. Its effect is indirectly expressed in the population fluctuation by emergences of insects and reproductive activity in other groups. This is admirably demonstrated in the sudden pupation and emergence of *Palpomyia*.

Temperature regulates the duration of the growing season and thereby profoundly affects the number of generations produced in groups like the Chironomidae. Actual length of the growing season for Big Shoal cannot be definitely set but it is approximately from mid-May to November. Some activity may take place before and after these date limits but very little.

Light, i.e., radiation, presumably exerts a definite influence on the bottom fauna. In shallow water areas, negatively phototrophic animals must either move to darker regions or avoid the intense light by burrowing. As will be shown later, the population on this shoal is an assemblage of burrowers. Although not definitely shown in this study, light may be a strong influence in determining the habitants of shoal water. It probably is partially responsible for the necessity of burrowing.

Bottom materials exert some influence on the distribution of organisms. Other factors in the dynamics condition this correlation to some extent. Noteworthy are the facts that *Limnodrilus* is most prevalent on areas composed of loose sand, flocculent marl and muck; *Amnicola* and *Gyraulus* abound on bottom which consists of sand, muck and dead shells; and *Progomphus* seems unusually well adjusted to the shifting sand bottom within the zone of greatest water agitation. Within rather wide limits, there is a certain assemblage of organisms for each water depth sampled. However, this assemblage may be the result of factors other than the slight variations in bottom composition.

The extent and severity of bottom movements influence the distribution of bottom fauna especially in shallow water. Small organisms, and larger ones to a lesser degree, are transported with these shifting bottom materials. The magnitude of this movement is illustrated by the finding of a large clam, used in an experiment to be described later, in one of the wooden frames set in the bottom to test the degree of bottom shifting. Experimental plots where the clams were located were at least thirty meters away. Migration of the clam into the frame was hardly feasible because of the impediment offered to the foot of the clam by the frame's wooden sides. It is the opinion of Lundbeck (1926) that currents move organisms from shallow to deeper water. The autumnal migration of forms into the profundal zone of South Fishtail Depression as described by Eggleton (1931) might be the result of such a mode of transport.

Water level fluctuation is a potent factor in the economics of organisms inhabiting shallow areas of Big Shoal. The water fluctuation during this study was 0.6 meter. Very few organisms were found at the 0.3- and 0.6-meter water depths during early spring. The gradual fall in level during the summer and autumn probably explains the shoreward migration which appears in the population table. Samples were taken at predetermined depth intervals regardless of water level. Hence, sampling was progressively pushed lakeward by the fall in water level.

Wave action is the most important single factor in the dynamics of Big

Shoal. To test the action of waves and the ability of mussels to maintain their position in such an environment, a series of experiments was conducted. On July 11, 1938, 45 *Lampsilis*, 32 *Anodonta* and 11 *Ligumia*, all of which were marked, were placed in a quadrat beneath 0.6 meter of water. A stiff northwest wind blew for 1.5 days following the start of this experiment. All mussels were in their original places on July 14, excepting two *Anodonta* which had lost their footing and were lying sidewise on the bottom. These clams were replaced in the bottom. After periodic storms between July 14, and August 8, 41 *Lampsilis*, 26 *Anodonta* and eight *Ligumia* were recovered from the original quadrat. One *Lampsilis* was found 23 meters away. One *Anodonta* was in one of the frames used to test bottom shifting 30 meters away. The remainder of the mussels were never located.

Another group of mussels consisting of 10 *Lampsilis*, 10 *Anodonta* and five *Ligumia* was placed in the bottom beneath 0.1 meter of water. Following the storm of July 14, four *Anodonta*, one *Lampsilis* and two *Ligumia* were found washed ashore. The remainder were in their original position although they were almost buried by beach cusps. This experiment was repeated on August 12, 1938. The following day after a brisk northwest wind the mussels were found in confusion although those individuals remaining in the quadrat were approximately in the same order as when placed there. Two *Anodonta* and two *Lampsilis* were on shore and two of the former genus were found rolling along in an alongshore current which was traveling at about 0.3 meter per second.

Results of these findings agree with observations of a similar kind made by H. B. Baker (unpublished) in Douglas Lake and given in tabular form by Welch (1935).

Water currents on Big Shoal affect the population in three different ways: transportation, bottom shifting and molar action. Wire mesh baskets were suspended in the water over Big Shoal and were found to become populated with organisms typical of shoal fauna and forms entirely foreign to it. The baskets at first collected sundry threads and filaments of disintegrating plants. As these accumulations became larger, organisms began to inhabit them. Predominant in the fauna thus collected were Chironomidae and Ephemeroptera all of which normally inhabit the shoal. Anisoptera and Trichoptera also occurred on the baskets. The former suborder was represented by at least two forms not inhabiting the shoal. The Trichoptera were normally present on the shoal.

Molar action, the result of wave and current energy, is particularly effective on the population of Big Shoal in shallow water (0.0–0.9 meter). It will be noted that *Progomphus*, a burrowing, heavily sclerotized nymph, inhabits the region of molar action exclusively. *Macromia* and *Hagenius* nymphs occur in this region occasionally but are not permanent inhabitants. *Chironomus*, Trichoptera and *Pisidium* are commonly found there. Each is well equipped to survive the grinding of the sand. To separate the effect

of molar action from all others cooperative with it is very difficult, hence it cannot be stated that molar action is *entirely* responsible for the exclusion of forms found elsewhere on Big Shoal.

Vegetation, although exceedingly limited, plays an important role in the environmental complex of certain groups of organisms. A comparison between the fauna in areas supporting *Chara* and the fauna in areas devoid of plants, both at the same depth, is interesting. For example, *Hydra* occurs only in *Chara* beds. The small Annelida, *Pristina* and *Stylaria* were practically absent from areas without this plant. *Limnodrilus* was almost equally abundant in both situations. An average of 22 *Amnicola* and 28 *Gyraulus* per square meter were found in the *Chara* beds while 85 and 291 individuals respectively were on the barren areas. *Pisidium* showed little preference for either area being present in almost equal numbers in both places. *Hyaella* abounded in the *Chara* patches. Four hundred and sixty of them were present in an average square meter of *Chara*-covered bottom while only 40 could be found in a similar area of sandy bottom. Chironomidae were almost equally distributed in both areas. The average number of organisms per square meter where *Chara* grew was 2613; that of like areas devoid of plants was 1984. Berg (1938) found that the presence of *Chara* increased the bottom fauna of sandy areas in Esrom Lake. He concluded that clean, sandy bottom areas at a given depth are about one-half as rich in numbers of individuals as areas at the same depth which are overgrown with *Chara*.

Life cycles of organisms on Big Shoal are influential in population changes. To discuss the life-histories of all forms present is not justified here. The 10 most numerous groups are presented below.

Cocoons of *Limnodrilus* appear on Big Shoal in July. The young were predominant in counts made of samples for mid-September. Practically all *Limnodrilus* taken in the spring were immature and not until mid June were sexually mature individuals numerous.

Amnicola produce one generation each year. The adults die off rather suddenly after laying eggs during July. This disappearance produces a seasonal low in mid-August but the young generation enlarges the population to a maximum for the year by mid-September.

Gyraulus reproduce about the same time as *Amnicola*. Their influence in population changes is not so marked since the adults do not die suddenly after laying eggs. One new generation is produced per season and exerts its numerical influence in sample counts during mid-September. Not much can be said about the decline in numbers of individuals in this genus, but their numbers are less in early spring than in late autumn.

The representatives of the genus *Pisidium* are ovoviviparous and no observations were made on the time of development or release of young. However, a distinct rise in average numbers per square meter began July 2 and continued until August 15. By September 15, a population decline had begun.

Few observations were made on the life history of *Hyalella*. Two periods of reproduction may be conjectured, one in July and another in September.

Young *Limnesia* appear in samples taken from Big Shoal during late August and early September. Adults lay their eggs in July. Some of the adults persist into autumn but the majority of the population is immature at that time.

Seasonal occurrence of pupae in five larger groups of dipterous larvae on Big Shoal is shown in Table 11. *Pentaneura* probably produces three generations yearly on Big Shoal; *Procladius*, two; *Tanytarsus*, three; *Chironomus*, two; and *Palpomyia* probably two. The effect of emergences on

TABLE 11. Totals and averages per square meter of some dipterous pupae on Big Shoal at each collection date.

Date	<i>Pentaneura</i>		<i>Procladius</i>		<i>Tanytarsus</i>		<i>Chironomus</i>		<i>Palpomyia</i>		Total
	Total	Ave.	Total	Ave.	Total	Ave.	Total	Ave.	Total	Ave.	
1937											
Oct. 9-10	—	—	—	—	—	—	—	—	—	—	—
Oct. 31	—	—	—	—	—	—	—	—	—	—	—
1938											
Apr. 23	6	1	—	—	20	2	—	—	—	—	26
May 8	—	—	—	—	—	—	23	2	—	—	23
May 14	—	—	—	—	49	5	10	1	—	—	59
May 28	2	—	10	1	125	13	77	8	—	—	214
June 17	13	1	55	6	622	62	475	48	2304	230	3469
July 2	—	—	2	—	102	10	304	30	106	11	516
July 16	—	—	—	—	35	4	173	17	17	2	225
July 30	11	1	14	1	336	37	649	65	9	1	1019
Aug. 13	8	1	12	1	275	28	198	20	52	5	545
Sept. 13	2	—	6	1	87	9	4	—	—	—	99

seasonal population is obvious. It is noteworthy that directly following each maximum of pupae, there is a corresponding decrease in the total population of the group from which they came.

GENERAL DISCUSSION

All environmental factors operative on Big Shoal are so interrelated that consideration of the effect of each one separately is a difficult task. Together they act to restrict the population, reduce the organic content of the bottom material and, in a broad sense of the term, eliminate those forms incapable of burrowing or otherwise protecting themselves. Even though beaten by heavy waves, stony beaches in Douglas Lake are capable of supporting different and more numerous species.

Studies of more protected but otherwise similar situations within Douglas Lake illustrate that most of the species common to Big Shoal are present there, but, in addition, many other species are well represented. In protected areas where sand is the bottom constituent and water depths are very shallow (0.3–0.6 meter), the species found far outnumber the species recorded from the most productive regions of Big Shoal.

From a consideration of the faunal list of Big Shoal, it becomes evident

that the organisms there, with the exception of those normally above the bottom, have the characteristic of burrowing as one of their habits. This burrowing is accomplished in diversified ways. Those species which do not actively burrow, build cases or slime tubes which are usually weighted or so made that they adhere to the bottom material. Examples of such adaptations are plentiful. Reference is made to the convex, hemi-streamlined cases of *Molanna*; the varied and multiformed cases of the several species of *Tanytarsus*; the slime tubes of *Limnodrilus* which appear studded over their entire external surface with fine sand grains; the tubes and cases of *Chironomus*. *Campeloma* and *Amnicola* burrow beneath the sand during periods of storm. *Progomphus* burrow actively and rapidly. *Ephemera* and *Hexagenia* burrow in the loosely packed, sandy, marly areas.

The small size of individuals in the fauna of Big Shoal is probably an asset to them. This smallness and the similarity in specific gravity of such individuals with that of water partially nullifies the effects of molar action and current transportation. In most cases, larger organisms inhabiting the shoal are protected by shells or are heavily sclerotized.

The term barren has long been applied to sandy, wave-swept areas such as Big Shoal. Compared with the rest of the littoral zone of Douglas Lake, Big Shoal is less productive. However, it is no biological desert as the term barren would indicate. Lundbeck (1926) and others find sandy shoals quite limited in production of bottom fauna. Berg (1938) states that sand flats in Esrom Lake are quite productive at water depths of 2.0 meters.

Douglas Lake has modified its shoreline considerably (I. D. Scott 1921). Changes now in progress are slower but just as certain as any which have taken place. Big Shoal is being gradually extended landward. Accompanying this landward extension, the shoal is being built lakeward into South Fishtail Depression and toward Grapevine Point. A narrow channel separates the shoal from this point but ultimately the channel will be filled. These changes may increase the productivity of Big Shoal.

SUMMARY

1. Of the factors operative on Big Shoal, wave action, currents, bottom composition, temperature, life cycles of the organisms and water-level fluctuation exert the greatest influence on the fauna. The most important single factor is wave action.
2. The bottom population is almost exclusively an assemblage of burrowers.
3. A differential in ability of mussels to withstand wave action, currents and bottom shifting is shown by experiments. *Lampsilis siliquoidea*, *Ligumia nasuta* and *Anodonta grandis* were found to be resistant in the order named.
4. *Chara* on the shoal bottom is definitely conducive to faunal increase.

By comparison of *Chara* covered bottom with bare sand areas at similar water depths the beneficial influence of holdfasts and shelters is demonstrated.

5. Numerically dominant groups in the bottom fauna are in order of their occurrence: *Tanytarsus*, *Chironomus* and *Limnodrilus*.

6. This type of shoal, although not as productive as most other kinds of littoral areas of Douglas Lake, is less of a biological desert than has been assumed.

7. Migrations of bottom organisms are due in part to bottom shifting.

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